

## THE TRAP OF UTRICULARIA CAPENSIS— HOW IT WORKS.

(With Plates VII—X.)

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Just previous to the meeting of the B.A.A.S. in Cape Town in 1929 I had the opportunity of studying the trap (usually and less preferably the "bladder") of *Utricularia capensis*, and ought at that time to have ascertained the facts which would have enabled me to interpret correctly its mode of action. I was then rather new to the game, for it was only in the previous winter that I had been able to show definitely that the traps in *U. gibba* and *vulgaris* (and by implication others of that type) act in a purely mechanical manner, conditioned by the watertight character of the door; and this I showed to be due to the presence of a membrane—a second valve in fact—sealing the chink between the door edge and the threshold on which it rests. The Cape Town opportunity enabled me to satisfy myself that what was in general true of *U. gibba* is also true of *U. capensis*. The anatomical facts observed and the behaviour of the trap in general were later published; but it must be admitted that only much later was an adequate understanding of the precise manner of working of the entrance mechanism attained. The first light was seen when the living material of *U. cornuta* became available and was studied in 1932 (Lloyd, 1933) that a definite hint as to the behaviour of *U. capensis* was had. This was completely verified by a study of living material of *U. Welwitschii*, grown for me from seed in the Edinburgh Botanical Garden (Lloyd, 1935). This species is like *U. capensis* except in the number and arrangement of the combs of glandular trichomes borne on the surfaces about the entrance. Nevertheless the opportunity to study *U. capensis* itself in the living condition (my chief purpose in visiting Cape Town) was not to be missed, and the effort to do so has been justified in the clarity of the evidence afforded, due in part to the unexpected translucency of its very small traps (0.5—1.25 mm. in length.) It is the purpose of this paper to give the results obtained.

### SHAPE AND DIMENSIONS OF THE TRAP.

The trap (pl. VII—1) is a hollow organ laterally compressed and neatly pear-shaped as seen from the side, with its stalk however attached in the middle of the thicker end. As thus seen, the opening into it is at

one side of the narrow end, and is circular (pl. VIII—2). The narrow end of the pear is flattened into a rostrum bearing six rows of stout glandular hairs radiating toward the centre of the opening: "upper lip fimbriated," as the taxonomists say. On the opposite side of the opening there are six rows of similar but stouter hairs, also radiating toward the centre of the opening ("lower lip fimbriated," though here a "lip" is not present). These hairs secrete mucilage to which mud particles, etc., may adhere abundantly. Their position suggests them to be guides flanking grooves along which minute animals are guided toward the opening which leads to a tube, as Miss Stephens (1930) called it, narrowing, when viewed laterally, toward the inside. One side (conventionally the upper) of the tube is occupied by a valve or door. The rest of the wall of the tube is divided into two regions, the forward (the forestep) lined with glandular hairs of graduated sizes, the outermost the longer; and the inner (pavement epithelium) clothed with crowded short glandular hairs, being more and more crowded towards the inside of the trap. This will be described more particularly beyond. The whole surface crowns a massive thickened portion of the wall, the threshold ("collar" of Darwin, though he did not see this species) since the door edge rests against it. The simple diagram herewith will enable the reader to visualize this (fig. 1).

If one looks directly into the entrance one will see that the glandular hairs lining the tube are placed radially, falling short of meeting in the middle (pl. VIII—2). They thus bar the entrance except for a narrow tubular passage formed by their ends. The effective passage so formed permits the entrance of minute animal forms, such as cyprids, nematode worms, etc., though the hairs can bend sufficiently to allow larger forms to enter, up to a certain limit. The outer surface of the door also bears glandular hairs of short curved form which complete the circle of the passage, or, when the trap is not in the set condition, block the entrance entirely (pl. IX—1, 2).

With regard to the remaining structural details of the trap it should be pointed out that the wall is in general composed of two courses of cells (there are more in the threshold), the outer of shallow cells, the inner of deeper ones (pl. VII—1, 2).

Surrounding the entrance the wall is considerably thicker, and, with the threshold (which is of course a part of the wall) can resist deformation by the side walls as they move in and out according to the changes in the water content of the interior. Scattered and inserted between the cells of the outer course are sessile glandular cells secreting mucilage and in similar situations on the interior occur glandular hairs with four transversely placed arms, called by Darwin quadrifids (pl. VIII—5); but on the

inner surface of the threshold, these are either simple or bifid (pl. VIII—7). The arms are cylindrical, bluntly ended. These internal glands are secretive (of digestive enzymes) and at the same time absorptive, this statement subject somewhat to the ultimate definite proof of the exact nature of the digestive process. All these hairs agree with the general type peculiar to *Utricularia* in consisting of a fundamental series of three cells, the basal, sunk into the epidermis, a small mid-cell, cutinized and small, supporting the end cell or cells devoid of cuticle, since it is easily thrown off, permitting in many cases of the secretion of mucilage. In some species (e.g., *U. vulgaris*) the quadrifids are extremely numerous; in other, as in *U. capensis*, quite few.

#### HOW THE TRAP WORKS.

We are now in position to examine into the precise working of the trap. First of all it must be understood that the walls have the power of excreting water from its interior. (Nold, 1934.) Since the trap is watertight (as we shall later see), this excretion results in a reduced volume of water in its interior, resulting in the partial collapse of the more extensive lateral walls so that in this condition they are concave, regarded from the outside.

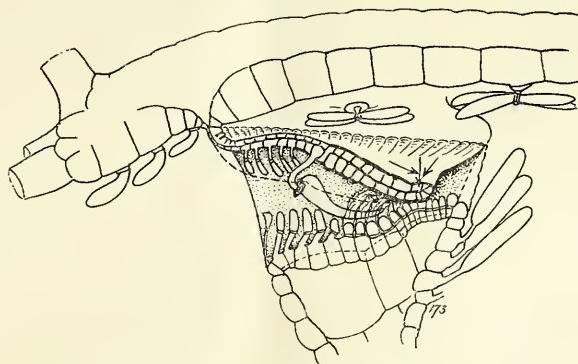


FIG. 1. Diagram of sagittal section of *U. Welwitschii*. The door in set posture. Broken line indicates the relaxed posture. Cf. pls. VIII, IX; figs. 3 and 4.

The collapse of the walls proceeds without distorting in the least the mass of tissues about the opening, which, as explained above, are more massive, and are jointed with the walls by a thinner hinge.

If one punches a minute hole through the wall with a needle point, water can gain access to the interior, when the walls bulge outwardly

and become strongly convex. (Merl, 1921). The whole system is now in equilibrium; the trap is relaxed. In this condition it is incapable of catching prey. When the walls are concave, on the other hand, the trap is in a condition of "unstable equilibrium" as Brocher (1911) first said; that is, the trap is *set*. This brings us to the question of how the condition of "unstable equilibrium" is maintained, and what happens when the trap is actuated.

We know that when the trap is set the outer water is pressing on every portion of the outer wall, including of course the valve or door. As compared with the relatively rigid wall, the valve is very flexible and tends to yield to the pressure of the outside water. While, however, it yields there comes a point when it yields no more, and as long as only the water presses on it, it remains in equilibrium (fig. 1, pl. IX, X). If, however, an uneven pressure is brought to bear on it, it can no longer resist the water pressure and it is momentarily forced open by the water which rushes in, sucked in by the outwardly springing wall, just as a compressed rubber ball will expand when released and suck in air or water through a hole in its side. Owing to the physical properties of the valve, being flexible but strong and having a set form, it closes again, cutting off the inrushing water at slack tide *before the walls are completely expanded*, but now comes into a different position, that which it takes under an approximately minimum water pressure. This is the relaxed posture (pl. IX—2; X—2) when it cannot act and the trap cannot catch prey. As the water is excreted from the interior—this goes on continually—the pressure of the outer water steadily increases, and the valve gradually comes into its original, that is, the set posture of "unstable equilibrium" ready to be again actuated. The process of excretion occupies, in *U. vulgaris* and other similar species about a half-hour, in *U. purpurea* about two hours. In *U. capensis*, judging from a few observations, it takes about an hour. Aside from the process of water excretion, the operation of the trap is purely mechanical, although it should be said that attempts have been made to show that the mechanism is an irritable one (Kruck) and it is to the credit of Darwin (Insectivorous Plants) that he rejected this view. The opening and closing movements of the valve are very rapid, the former about four times as rapid as the latter (since the closure is against inflowing water). In *U. vulgaris*, as ascertained by means of moving pictures taken at the rate of 160 exposures per second, the opening takes one frame ( $1 \cdot 160''$ ), the closing  $4 \cdot 160''$ , in all  $1 \cdot 32''$ , an exceedingly rapid movement. That a plant organ should be capable of making such a rapid movement of displacement and restoration is most astounding, when, as we know, plant cells are clothed with a cellulose wall. So far as I know the only movements comparable in point of speed

are those of cilia and flagella in protista. Other movements due to irritability (leaf movements of *Mimosa*, stamens of *Berberis*, stigma lips of *Diplacus*) are very slow in comparison: while results due to mechanisms set up in ripening fruits causing the ejection of seeds act rapidly, they are due to the action of ejecting pollinia, of dried dead parts under tensions. The action of the fruit of *Impatiens* and of parts of the flower in some orchids are similar, but here the walls are still living. In all these, however, the action is irreversible. It is worth while to endeavour to understand the entrance mechanism, that is to say, the minute structure of the valve and threshold (for they work together) in order to form an adequate conception of how all this behaviour is accomplished.

It was for long thought that the door in *Utricularia* acts as a simple check valve, comparable to the check valves of our veins (but here they are double), and that prey, attracted by some lure (mucilage probably) made its entrance by pushing up against it (fig. 2). After passing in, the

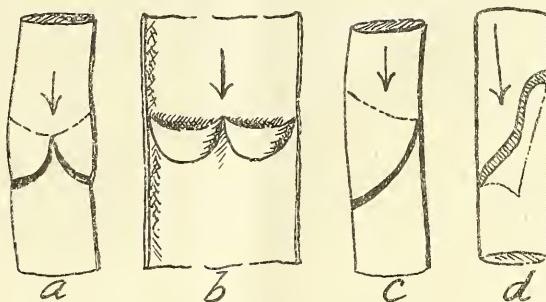


FIG. 2. Diagrams of simple check-valves in the veins (a, b), an imaginary single check valve in a vein (c) and (d), the door or valve of *U. capensis*. Arrows indicate the direction of flow of blood which is prevented. In (d), the flow is not prevented unless there is a special mechanism to stabilize the door.

valve fell passively into place and prevented exit. Darwin, Cohn and many others held this view, and it is the one prevalent in textbooks even now. Small in his text book affords an exception. It was not till 1911 that, as the result of the observations of the entomologist Brocher of Geneva, it was clearly indicated that this idea was untenable. He saw that there was a reduced pressure of water in the trap, which could not be the case if the door is a simple check valve; and further, that the door must be watertight, but his idea of the mechanism involved was incorrect. Nevertheless he observed that the prey is caught instantly (as indeed had Darwin) but, though he suspected that the action could be repeated, did not find out if this is the case. This observation was made first by

Merl (1921) and then by Czaja (1922) who timed the intervals between possible actions, the minimum period Merl found, for *U. vulgaris*, to be 15 min., but this is unusual, 30 min. being usual. It is evident from such observations that the *Utricularia* trap valve can offer resistance to the mass movement of water under pressure tending to flow in the direction *opposite to that in which it should go* to be checked by a simple check valve (fig. 2).

We now ask ourselves the question, what sort of mechanism can succeed in doing this. As pointed out above the entrance of water is not gradual ; it does not ooze in, but rushes in suddenly and in a large stream, which is eventually stopped by the back movement of the valve *before the walls of the trap have expanded to the full*. That is, the valve has an intrinsic tendency to assume a certain posture, just as has the roof of a bowler hat : it is in fact of a certain definite shape which in itself procures closure of the passage against the flow of water, *if the pressure is not too great*. If we dissect away a door we find that its shape is retained even after separation from the trap. If the pressure of water is increased (as it must be on exertion of water from the inside of the trap) still water cannot leak in under the edge of the valve ; even the available maximum water pressure *alone* cannot do this. Since when water enters, it does so suddenly, we may believe that a latch of some sort has been brought into action. Where is the latch ? In order to make the problem clear by means of an analogy, imagine a door supplied with a slip latch<sup>1</sup> —the kind which gives when one pulls on the door hard enough without the necessity of turning a knob. It is obvious that such a door when closed would withstand a certain wind pressure, but a blast of a "black south-easter"<sup>2</sup> would blow it open and the opening would be sudden. If the door were provided with a spring, it could close against some wind pressure, so that the analogy is complete, except for the fact that the *Utricularia* door is not flat and rigid, but a flexible valve. This brings us to the precise question of the construction of the door or valve.

#### THE DOOR.

A dissected-out door when pressed out flat—(having a set form it does not of itself become so)—is roughly triangular, rounded at the narrow end, the broad edge slightly scalloped into three reaches, the middle and two lateral (fig. 3). It is quite evidently divided transversely into two regions, the upper (at the apex of the triangle) and the lower, all the rest, the line of division being above the middle point, so that the upper region

<sup>1</sup> Called a "Bayle's latch" in the furniture trade.

<sup>2</sup> Capetown's boisterous summer wind.

is the smaller. The upper region is seen to bear a group of rather closely packed, short, downwardly curved glandular hairs (fig. 1); and at the lower edge of the group there is a single large hair having the shape of a Malay kriss, hence called the "kriss trichome" (pl. VII—4; fig. 1, pl. VIII—9). The lower region is smooth.

Again, when the door is relaxed and under no restraint, the upper region is concavo-convex, convex outwardly with respect to the interior of the trap (figs. 1, 3). The hairs are therefore on the convex

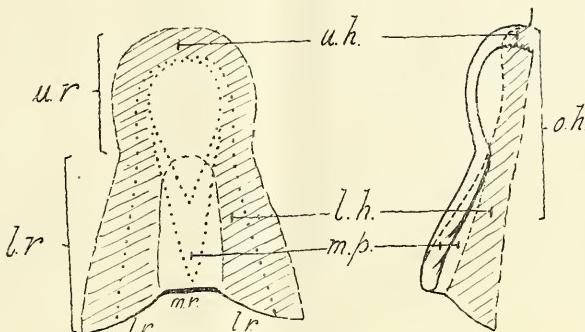


FIG. 3. Plan of door in *U. capensis*. u.r., upper region ; l.r., lower region ; u.h., upper hinge ; l.h., lateral hinge, together constituting the outer hinge. Dotted lines indicate the curvatures of the door on opening. l.r., lateral reach of door edge ; m.r., middle reach of door edge. Broken line (right-hand fig.) indicates the set posture of the door.

surface. The lower region is circularly curved transversely (pl. VIII—8), the curvature corresponding in form to that of the threshold on which the door edge rests. In the third place the upper region is thin (pl. VII—4), the lower thick, consequently the former more, the latter less, easily bent. All parts are quite flexible and can be bent into all degrees of curvature with complete recovery on release, in which respect the tissues are highly peculiar. One is reminded of the annulns of ferns, or the mechanical tissue of anthers, but neither of these behaves as does the *Utricularia* door. The explanation of this is to be found in the minute structure.

In the first place the walls of the cells appear to be highly flexible. Chemical tests have so far failed to reveal any differences as compared to ordinary cellulose walls, but much handling in an experimental way indicates that there are. Pure cellulose walls when wet are of course rather flexible in any case.

In the next place the forms of the cells contribute very largely to the flexibility. The whole door is composed of two courses of cells, an outer (with respect to the trap as a whole), which is histologically continuous with the outer course of cells of the trap wall (fig. 1); and an inner, continuous with the inner course of wall cells. The door is indeed a thin outgrowth of the trap wall. In the outer zone of the upper region the outer cell course is very thin indeed, becoming thicker as the lower region is reached. Conversely the inner course is thicker in the outer zone, and is on the inner surface deeply corrugated concentrically with respect to the outline of the door. The cells themselves are rather longer than broad, their major axes arranged radially. There is thus produced a bellows structure which gives great amplitude of bending movement precisely where the greatest flexibility is needed. Similarly the outer lateral zones of the lower region exhibit a similar structure, the whole outer zone of maximum bending constituting a sort of hinge, the outer hinge (pl. VIII—8; fig. 3).

The middle area of the upper region can bend, but not sharply, merely becoming concave (when the trap is set) or convex when relaxed (fig. 3). There is of course no sharp line of demarcation between the hinge and middle area.

The lower area is much thicker than the upper and has thicker walls and very deep corrugations; somewhat oblique to the axis of the door and approximately parallel to its line of attachment to the wall. Its middle area (the middle piece), the lateral limits of which are indicated by the extent of the middle reach of the free edge, is the thickest and more massive, and is capable of sharp bending along its axis (fig. 4). My

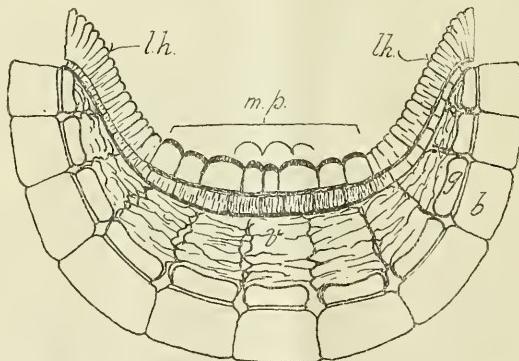


FIG. 4. Diagram of transverse section of entrance to show the deep corrugation of the middle piece, and the cells of the pavement epithelium providing the velum. g., gland (capital) cell; b., basal cell. The thin cell between is the mid-cell. v., velum; m.p., middle piece with deep corrugations; l.h., lateral hinge.

photographs of *U. Welwitschii* (pl. VIII—8) taken transversely through the door in this region indicate that there is a line of greater flexibility along the axis due to the meeting of deep parallel corrugations; the same is true of *U. capensis*, so that when the door opens under water pressure there can occur a momentary sharp longitudinal bending, leading to a reversal of curvature during the initial rush of water.

All the cells of the door have this in common, namely, that lateral (anticlinal) walls are very thin but are supported by numerous local thickenings, called props (Meierhofer: *U. vulgaris*, 1902) placed at right angles to the general surface of the door (fig. 5). The thin walls are easily bent but the collapse of the cells when under the strain of bending is prevented by the props. In the living door the cells are of course under

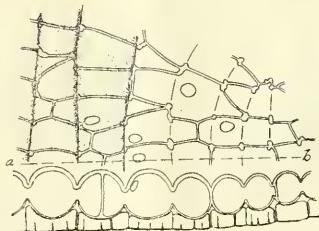


FIG. 5. Diagram to indicate the structure of the walls (in *U. vulgaris*) giving the bellows effect.

turgor pressure, and, since the sap is non-compressible, the thin walls by bending and stretching allow the transmission of pressures in any necessary direction. The outer walls, forming the surface of the door, are thicker, the bending movements being facilitated, as above said, by the corrugations which afford a bellows effect. While, as said, the hinge zone of the lower region is highly flexible the outer course of cells being thin and the inner corrugated, in the middle part opposite the middle reach, the courses are of approximately equal thickness, and the whole quite massive. This is called the middle piece, and is of importance in receiving the lateral thrust of the lateral hinges, so maintaining the posture of the lower region when the trap is set (fig. 4).

#### THE THRESHOLD (pl. VIII—1, 7, 8).

We must now glance at the threshold. This term is applied to that mass of tissue supporting the entrance mechanism and continued as a thick mass of tissue surrounding the entrance. It is lined on its curved

surface with glandular hairs of various kinds in regard to size and function. This surface when seen in transverse sections of the trap spreads around *ca.* 2/3 of the surface at the outer opening (pl. VIII—2) and one-half at the inner. The oblique lateral lines of limit are the lines along which the attached edge of the door lies. The passage from outer to inner opening is, however, not cylindrical, the inner opening being the narrower; nor is the gradient a continuous one, but is marked by three changes (pl. VIII—1), each stretch occupying about one-third the distance from outer to inner opening. The first (the forestep) is *ca.* parallel with the roof, and is lined with rows of stalked glands, longer at the opening and shortest at the inner limit (fig. 1; pl. IX—1). Beyond this the floor rises at a slight angle (so that the transverse section of the

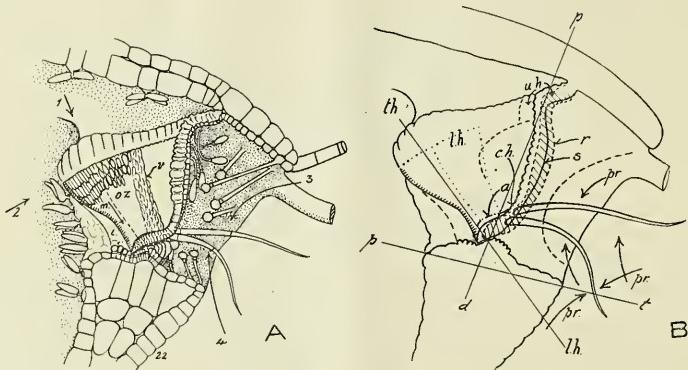


FIG. 6. (A) Diagram of the entrance mechanism in *U. gibba*. v., velum; o.z., outer zone of pavement epithelium; m., its middle zone and i., its inner zone. Arrows 3, 4 indicate the direction of movement of prey in touching the bristles and so activating the trap.

(B) Diagram showing how the door is stabilized when under water pressure. s., set; r., relaxed postures. a., disturbed posture due to touching of the bristles in directions pr. P.d., thrust of door; th-lh. thrust of lateral hinges (l.h.); p t, general level of the threshold; e. h., central hinge.

entrance becomes narrower) and is clothed with rather closely-packed sessile hairs (pl. VII—4), the cuticles of the outer or capital cells of which are much expanded or ballooned, and constitute collectively a valve-like filling, the velum, which plugs the angle between the door and the threshold and makes it watertight. It was first observed by me in 1929 in *U. gibba*, and it was this that led to the reinvestigation of the whole entrance mechanism. The membranes are very diaphanous, and easily escape observation. The velum occupies the outer zone of the pavement epithelium (fig. 7 : pl. VIII—7). The rest of the pavement

epithelium is composed of the middle and inner zones. The former is characterised by very small compact glandular cells, and is narrower in the middle and broad at the sides of the threshold, supplying a firm and compact surface on which the door edge rests, contributing to the watertight closure. It has a slight tilt toward the outside of the trap so that it continues the gradient of narrowing. Beyond this is the inner zone of the pavement epithelium, narrow crescentic in form, and of negative value so far as we can see. The horns of the crescent coincide in position with the ends of the door edge.

The difference in posture of the whole door when the trap is set and after actuation, *i.e.* in the relaxed posture, will now be described. These different postures are to be seen in the accompanying figures, taken of living traps before and after actuation, in Jan., 1936, at Cape Town (pl. IX, X). Such figures as these are obtained by focussing the lens (4—16 mm.) in the sagittal plane of the trap so as to get a silhouette of the door and threshold. Because of the thickness of tissue through which the lens has to penetrate one cannot expect more than meagre clearness. One must be satisfied if one can make out the mere outline of the door and threshold as seen laterally. Of four pairs of negatives I have chosen the best for my purpose, while the diagram (fig. 1) furnishes a composite together with details only seen in good sections.

By comparing the two pictures in each of pls. IX and X, one of the set condition of the trap and one of the relaxed, it can be clearly seen that the upper region of the door is convex (looking from the outside) in the relaxed posture, and concave in the set. This can only be explained as the effect of differences of pressure of water on the outer surface. Since the upper and lower regions are not separated by a sharp differentiation of tissue it follows that the concavity extends somewhat into the lower region, the curvatures being harmonic. The effect of the concavity is to raise the upper part of the lower region, and so to tilt the whole into a position in which the axis of the door lies at a greater angle with the surface of the threshold so that the thrust of the middle reach of the door on the threshold is more direct. Contributory to the production of this thrust is that of each side of the door exerted transversely and these three thrusts taken together are sufficient to bring the whole door edge into firm contact with the middle zone of the pavement epithelium. It seems probable too that the strains set up by the convexities of the door result in moving the door edge slightly back (toward the inner opening), allowing the whole edge to lie smoothly by cramping it against the pavement epithelium.

In this posture the door is sufficiently raised (except, of course, at the edge) to leave an opening between the stalked hairs of the forestep and those of the upper door region, through which small animals can pass into a larger space beyond, in which they can move about. Being in such a confined space, the animal (a daphnid, cyprid, or other) moves vigorously and with sufficient energy to disturb the equilibrium of the door in its strained posture. This is by contact with the kriss hair.

I am able at long last to make this statement without fear of contradiction. Excellent material<sup>3</sup> brought from the Cedarberg at 4,000 ft. altitude by Professor Compton gave me the requisite opportunity for experiment as follows. I have elsewhere pointed out that the kriss trichome during development is directed toward the interior of the trap. In the mature trap, however, its position may become reversed, and the free end then is directed outward (pl. IX, X) and now lies in the narrow channel between the ends of the stalked trichomes and those clothing the upper region of the door. In this position it sticks out beyond the mouth of the channel far enough to be touched by a needle point. If, therefore, a trap with the kriss trichome in this position can be stimulated mechanically *without introducing the needle point into the entrance*, rather merely by moving it laterally across the mouth, it can be concluded that the kriss hair is the trip-mechanism. If, however, this movement of the needle does not produce results, and it must be introduced carefully so that the point enters *no further than the base of the kriss hair*, and moving toward the door, to result in actuation, this would be expected if the kriss hair is inwardly directed. Actuation when the needle did not enter the mouth was called position 1; when it was introduced as far as the base of the kriss hair and if then moved toward the point at which the kriss hair is inserted, this was called position 2. Of 42 perfectly clear and successful operations, 12 traps were actuated with the needle in position 1; 37 with the needle in position 2; and three cases as the needle moved from position 1 to 2. Many other cases were seen in which actuation occurred, but the course of the operation with the needle was not perfectly clear. Often the point of the needle is swallowed by the trap, and though it is perfectly clear that actuation has occurred, the movement is so rapid that it disturbs judgment. It seems quite clear, therefore, that the kriss hair is a trip-mechanism.

When actuated, the pressure of water can then be exerted to extend the concave curvature, and this then involves the middle piece throughout

<sup>3</sup> The plant brought in differs from that found in the vicinity of Cape Town by having linear leaves.

its length (fig. 3). There is a momentary longitudinal fold made possible by the deep longitudinal corrugations of the middle piece and in spite of the lateral thrusts of the lateral hinges on the door its transverse curvature is inverted. The water having rushed in, the tide slacks and the door by its own springiness closes again, but now comes into the relaxed posture.

In this posture the upper region is convex, and the lower region makes a narrower angle with the threshold, including of course the pavement epithelium. The angle is filled with the velum (fig. 1; pl. VII—4), and the whole is watertight under the diminished difference of pressure as between in- and outside the trap. As the excretion of water from within proceeds, the door gradually passes into a renewed set posture in which it again becomes mechanically sensitive, that is, in "unstable equilibrium."

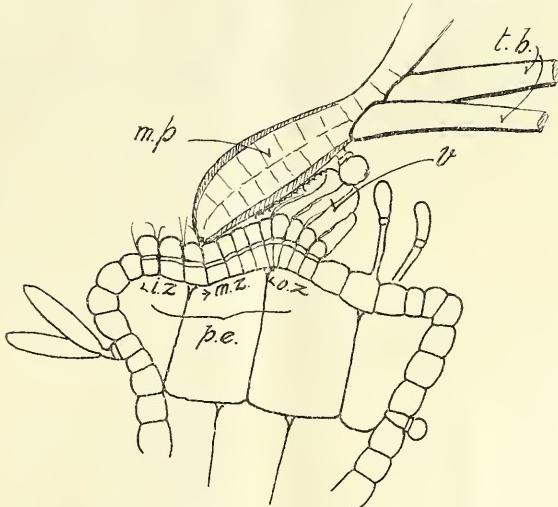


FIG. 7. Diagram showing the posture of the door edge in relation to the pavement epithelium in the set posture. t.b., tripping bristles; v., velum; o.z., m.z. and i.z., outer, middle and inner zone of the pavement epithelium. m.p., middle piece.

#### THE TYPE U. VULGARIS (figs. 6—8).

In my previous paper in the JOURNAL OF THE BOTANICAL SOCIETY OF SOUTH AFRICA, I based my interpretation of *U. capensis* on what I then knew of traps of an undetermined species (*U. gibba*, aff.), a plant

growing in the McGill University glasshouses, and related to *U. exoleta*, *U. vulgaris*, etc. Recent studies during the last two or three years have led me to correct my earlier descriptions in an important detail, and I take this opportunity to offer a correction.

This relates to the posture of the middle reach of the door edge in contact with the pavement epithelium. I previously described it as resting against the outwardly sloping surface of the outer zone of the pavement epithelium. Unfortunately the form I was working with lent itself too easily to this interpretation of the matter, and it was only after making use of a new method of attack that I discovered the mistake. This was to make photographs in set and relaxed postures at right angles to the sagittal plane of the trap so as to get an image of the profile of the door on the negative. It is, however, very difficult to get the entire profile owing to the amount of tissue to be penetrated optically. After a good deal of experience it was finally found possible to get at the facts.

In the set posture the edge of the door in the middle reach rests against the outer edge of the inner zone, which, because of a slight outward tilt, offers resistance to the inswing of the door. This is enhanced by the downward thrust of the door edge due to the inherent thrust of the door amplified by the pressure of the outer water upon it. In this position, the outer face of the middle piece of the door rests against the middle zone of the pavement epithelium, pressing outwardly, thus

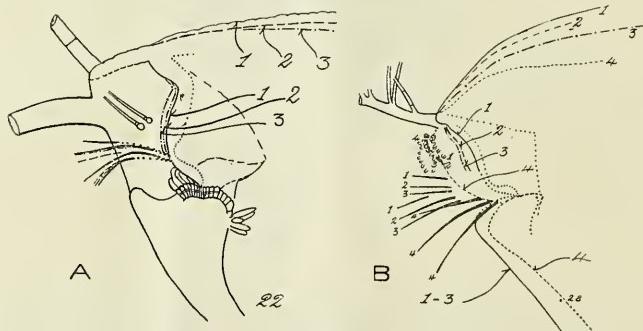


FIG. 8. Postures of the door in (A) *U. gibba* and in (B) *U. vulgaris*. 1, set; 2, relaxed (after normal activation) and 3, fully relaxed after puncturing the wall of the trap 4, in sagittal section.

making a tight joint, the watertightness of which is rendered complete by the velum which occupies, in the form of a bolster, the space between the base of the trip-bristles and the pavement epithelium.

The trap is actuated by lateral pressure on the trip-bristles in any direction. This distorts the middle piece and renders nugatory the downward pressure of the door edge, and the door, folding longitudinally under the water pressure, swings inwardly, returning swiftly back against the relaxing water current to the relaxed posture. To the eye, this is the same as the set posture, but careful measurements of projected images from lantern slides enable one to see that the profile of the door now stands a little forward (towards the opening of the trap) and the middle piece, resting with outward pressure against the middle zone of the pavement epithelium, aided of course by the velum, makes a watertight joint. In order that the pumping action of the walls may be effective at once, the door mechanism must be watertight *all the time*, but this does not mean that the door edge must rest firmly against the inner zone of the pavement epithelium. This condition is attained only as the water pressure increases towards its maximum. One must admit that it has been impossible to say precisely where the door edge rests in the relaxed posture of the door. The difficulties of observation are very great. But the forward position of the whole door profile makes it certain that there must be some difference, however small. In the diagram herewith (fig. 6B) this difference is probably exaggerated (cf. fig. 8.)

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#### PLATES.

PLATE VII. 1, Trap of *U. capensis* with door in set posture ; 2, the same after activation ; 3, check on retouched picture, plate X, fig. 1 ; 4, door of *U. capensis* in sagittal section.

PLATE VIII. *U. Welwitschii*. 1, Sagittal section of entrance mechanism. 2, Looking into the entrance : pointer indicates the door (upper region) ; 3, 4, set and relaxed posture of door taken from life ; 5, 6, outer and inner surface of door ; 7, looking down on the pavement epithelium ; 8, transverse section of door through the middle of the middle piece. 9, the kriss trichome.

PLATE IX. *U. capensis*. The door in set posture, with the kriss trichome showing projecting beyond the mouth of the entrance (retouched) ; and (lower picture) door in the relaxed posture.

PLATE X. *U. capensis*. Another case more highly magnified initially. The outlines of the door can be traced with considerable clearness in these pictures. The end of the kriss trichome has been retouched. See check on plate VII, fig. 3.